

THE INFLUENCE OF AGE AND FOOD DEPRIVATION UPON THE HOARDING BEHAVIOR OF RATS

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How does the number of food pellets hoarded by a rat in half an hour vary with the age of the rat? We should like to know something about this relation (*a*) because the curve of hoarding vs. age should shed light on the general problem of hoarding, and (*b*) because, without such knowledge, we cannot compare the results of hoarding experiments in which the subjects were rats of different ages.

PROCEDURE

In order to keep the independent variable *age* separate from previous experience in the hoarding situation, we tested seven different groups of rats, one group at each of seven age levels, instead of testing the same rats again and again. Rats from ten litters, raised especially for the experiment, were assigned to the seven groups in such a way that there was one rat from each litter in each group and each group consisted of five males and five females. Except for these restrictions and for replacements of a few rats that died during the experiment, the assignments of rats to groups were random.

The rats lived in small cages with their mothers until weaning at age 21 days. From that time until five days before their initial tests, the males and females were kept separately in large cages, about 15 rats per cage. The five days before the first tests were devoted to familiarization with the home-cage part of the hoarding apparatus, which was essentially the same as that used by Licklider and Licklider (7, Fig. 1).

Hoarding tests were started with the rats of Groups I through VII, respectively, on their 26th, 33rd, 42nd, 67th, 109th, 231st, and 318th days of age. The sequence for each rat was:

- (1) five daily $\frac{1}{2}$ -hr. tests,
- (2) two days of total deprivation of food,
- (3) five more daily $\frac{1}{2}$ -hr. tests.

From birth through period 1 and during period 3, the rats had plenty of food (Purina Laboratory Chow) in their cages, the deprivation period (2) actually being the $47\frac{1}{2}$ hours from the end of the fifth to the beginning of the sixth hoarding test. Water was always available.

We ran the hoarding tests in the evening, as near 9 o'clock as convenience permitted. By removing the barricade from the entrance to the alley, we gave each rat free-run of its hoarding apparatus and, thus, the opportunity to carry pellets from the bin to the home cage. The pellets in the bins were of Purina Dog Chow, very nearly the same in composition as the Laboratory Chow, but smaller and therefore easier for the young rats to carry. At the start of each test, there were 100 pellets in each bin.

RESULTS

The trend of hoarding with increasing age is shown separately for the pre- and post-deprivation tests in Figure 1. The ordinate scale is linear in number of pellets hoarded (N_p), and the abscissa scale is linear in age (t). Although the group means appear to fluctuate considerably with respect to whatever might

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be regarded as the "true" or parametric functions, it is clear (a) that at least some of the rats hoarded a considerable number of pellets without deprivation, (b) that on the average, however, the rats hoarded at least twice as much after deprivation as before, and (c) that under either condition the function relating hoarding to age is a negatively accelerated, increasing function.

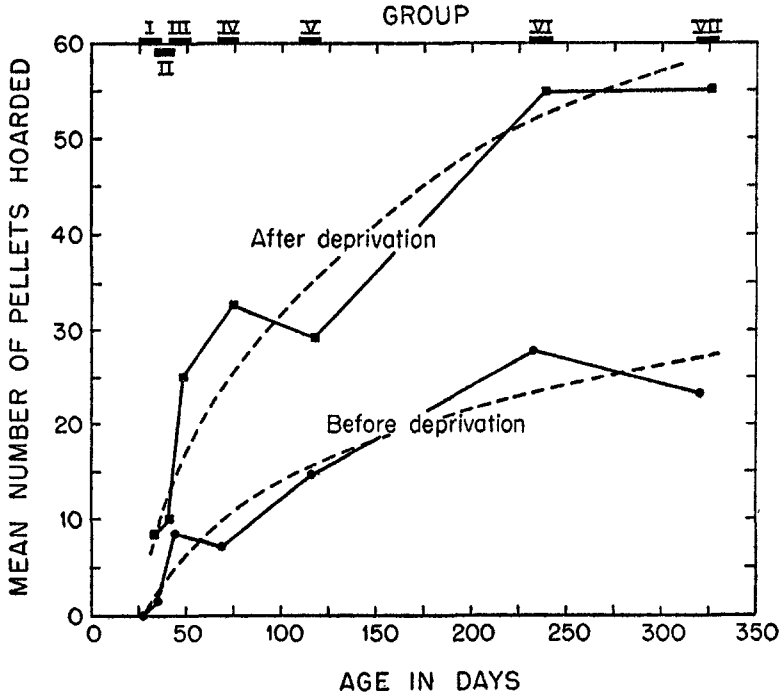


FIG. 1. HOARDING AS A FUNCTION OF AGE

The datum points show the mean numbers of pellets hoarded per half-hour test by the rats of the seven age-groups. The dotted lines are logarithmic functions of age.

THE COURSE OF THE FUNCTION RELATING HOARDING TO AGE

The dashed curves of Figure 1 express at least approximately the general trends of the functions relating hoarding to age. Since the dashed curves are of the form

$$\bar{N}_p = k \log t + c,$$

it follows that the empirical functions can be linearized approximately by plotting the graphs with a logarithmic, rather than a linear, age scale. (Taking the logarithm to base 2 of age in units of 21 days—21 days is the age of weaning—we have plotted the pre-deprivation curve with $k = 7.6$ and $c = -3$, the post-deprivation curve with $k = 15.7$ and $c = -3$.) Considering the variability of the data,³ however, we should avoid drawing from the present observations the

³ A table showing the number of pellets hoarded by each rat on each test has been deposited with the American Documentation Institute. Order Document 3236 from the American Documentation Institute, 1719 N Street, N.W., Washington 6, D.C., remitting

conclusion that hoarding increases exactly with the logarithm of age. It could as well turn out that the number of pellets hoarded is proportional to the weight of the rat or to his daily food intake.

DISCUSSION

Hoarding without Deprivation

The fact that some of the rats hoarded without previously having been deprived of food is in line with the observations of Wolfe (15, Experiment 1), of Bindra (1, 2), and of Licklider and Licklider (7). However, since the role of deprivation in hoarding (whether deprivation is a necessary or merely a facilitating condition) is a key question in the general problem, our confirmation of hoarding without deprivation should be examined carefully.

On the positive side, it can be noted that our rats hoarded unsweetened pellets without wrappers, and that some of the pre-deprivation hoarding was avid. In Bindra's experiment, by way of comparison, the mash in the bottle caps was sweetened with saccharin, and since only 8 capfuls were available to each rat in each test, the scores were not far above 5, which is the smallest score Morgan, Stellar, and Johnson (11) recognized as indicative of hoarding. In the experiment of Licklider and Licklider, the rats carried enough pellets to warrant without question the use of the term "hoarding," but some of the diligence of the rats was attributed to the fact that half the pellets were covered with aluminum foil. The present tests therefore confirm not only that rats will hoard without deprivation, but also that, under favorable conditions of age and environment, rats will hoard ordinary pellets actively.

On the negative side, we must admit that when we say "without deprivation," we can mean only that we made sure that there were always plenty of pellets in the cages. We could not rule out competition among littermates before weaning, and we did not supplement the diet of Chow with other foods.⁴ However, we convinced ourselves by observing and weighing the rats that, until deprivation was introduced intentionally into the experiment, they ate plenty of pellets—hence they did not suffer "depletion" (11) of any food component provided by the Chow—and that they grew at a normal rate.

It is noteworthy that the young rats of Groups I and II hoarded almost no pellets until they had been deprived of food. Their behavior after deprivation indicated that their failure, two days earlier, to hoard when satiated had not been due to inability to handle the pellets. Even after deprivation, however,

\$1.00 for microfilm (images 1 in. high on standard 35 mm. motion picture film) or \$1.00 for a photocopy (6 x 8 in.) readable without optical aid. The last-named author also has several copies of the table, which he will furnish on request.

⁴ Wolfe (15, p. 100) quotes a bulletin of the Ralston Purina Company as recommending the Dog Chow that Wolfe used as a complete ration, but as suggesting that breeding rats do slightly better when fed, in addition, a little cabbage or lettuce. However, with reference to the Laboratory Chow on which our rats were raised, Mr. H. L. Willeke, Assistant Director of the Ralston Purina Research Department, writes, "We do not recommend supplementation with anything but water." The chemical compositions of Purina Chows are described on p. 19 of the booklet, "The Purina Program for Laboratory Animals."

Groups I and II afforded few instances of truly active hoarding. It appeared that the low scores of the young rats were due not to lack of muscular development, but to relative inexcitability of the pattern of behavior involved in hoarding.

Three explanations for the inexcitability of the hoarding mechanism in young rats suggest themselves: (a) Hoarding is instinctive (10, 11), but the mechanism underlying the instinct must mature. (b) Hoarding is a learned reaction (14, 15), but the young rats had had little opportunity to learn it. (c) Rats are "wired" in such a way that, under favorable circumstances, they will hoard items that they value (3), but it takes experience (e.g., competition, deprivation) to make the pellets valuable. Our observations do not discriminate among these alternatives. They do, however, eliminate the possibility that food-hoarding is an instinct that appears full blown as soon as the rat can carry small objects.

The Influence of Deprivation

The marked increase of hoarding in the post-deprivation tests was expected, of course, on the basis of previous observations (1, 2, 4, 5, 7, 10, 11, 14). What we did not expect, as a matter of fact, was that we should have to resort to deprivation at all. Actually, we wanted to avoid it because, except in the case of zero deprivation, equality of deprivation for rats of different ages is subject only to arbitrary definition, and we were reluctant to limit the generality of our results by injecting unnecessary arbitrariness into the plan of the experiment. As it turned out, however, the introduction of food deprivation may be said to have made the results of somewhat greater generality than they would otherwise have been. The post-deprivation hoarding of the young rats suggested strongly, as we have noted, that they had been physically capable of hoarding even when, before deprivation, they had not hoarded. In addition, the fact that the pre- and post-deprivation curves of Figure 1 follow roughly similar courses makes it appear unlikely that the general shape of the function relating hoarding to age is highly dependent upon the particular conditions of measurement.

In order to understand the role of deprivation in hoarding, it is important to know why deprivation was required to make the rats hoard more than a few pellets in the experiments that appeared between Wolfe's (15) and Bindra's (1, 2), whereas in Bindra's, in Licklider and Licklider's (7), and in the present one, deprivation was not a necessary condition. (Deprivation was not *always* a necessary condition in the experiments of Morgan *et al.* Three of the 12 nondeprived rats that McLeary and Morgan [8] tested in a refrigerator hoarded approximately 14 pellets each in 24 hours. And 2 of 9 "satiated" animals, presumably never deprived, achieved scores as high as 20 pellets per half-hour in an experiment of Stellar and Morgan's [14]. With these exceptions, however, there was essentially no hoarding without deprivation.) Bindra has emphasized the importance of those characteristics of the hoarding apparatus that make the rat feel "secure" or "insecure," either about itself or the pellets. The openness of the alleys was one of those characteristics, and "secure" rats hoarded more on open boards than in closed runways. Stellar (12) has shown, furthermore,

that illumination is an important factor, that lighting the home cage decreases hoarding, whereas lighting the alleys increases it. It is reasonable, therefore, to conclude that our wire-mesh hoarding apparatus with shaded cage and illuminated bin provides a situation in which hoarding appears much more readily than it does in the closed alleys used in the earlier experiments, and that the facilitating effect of food deprivation is necessary to produce hoarding in the wire-mesh apparatus only when the rats are young and their hoarding mechanisms are relatively difficult to excite.

The formulation just given is, we believe, essentially the correct one but, until we saw the results of the present experiment we were not sure that the key to the deprivation problem was not the age of the rats. In Table 1 are shown the ages and the mean hoarding scores of all the nondeprived rats of specified ages except Wolfe's (15), that to our knowledge have been observed in laboratory

TABLE 1
AGES AND HOARDING SCORES OF NONDEPRIVED RATS IN PREVIOUS EXPERIMENTS

EXPERIMENT	AGE OF RATS AT BEGINNING OF TESTS	MEAN NUMBER OF PELLETS CARRIED
Hunt <i>et al.</i> (5).....	235	0.1
Hunt (4).....	219	0.7
Hunt <i>et al.</i> (5).....	157	0.1
Hunt <i>et al.</i> (5).....	136	1.3
Stellar and Morgan (12).....	ca. 80	2.4
Morgan <i>et al.</i> (9).....	ca. 66	0.0
Bindra (2)*.....	ca. 60	3.5
Licklider and Licklider (6).....	39	31.3

* Fifteen-minute tests.

hoarding situations. On the basis of the tabulated data—and knowing that the young rats in the last line had reached a peak of activity at the end of the first week of their daily task and then had hoarded less and less as time went on—we thought it just possible that young rats hoard in play, whereas older rats require the motivational boost provided by deprivation. Now, however, with the present data on hoarding as a function of age, we can be sure that any inverse relation between hoarding proclivity and age that we may infer from Table 1 is spurious.

The Significance of Wolfe's Results

Inasmuch as our principal points have been (1) that hoarding increases with age and (2) that deprivation is not a necessary condition for hoarding, it seems only fair to go back for a moment to the first of the series of papers on the hoarding behavior of rats that have appeared during the past decade. In that first paper, Wolfe (15) surmised that hoarding might increase with age:

It is possible that the greater age [63 days] of these animals was responsible for their carrying more than did the younger rats [40 days of age] which likewise had been on an inadequate diet for twenty days (p. 106).

In the same paper, Wolfe described the results of observations on nondeprived rats: "... ten adult rats, around 120 days old, in the cages of which dog chow had always been present" (p. 99). These rats were allowed to hoard on open boards for 30 minutes at a time. The mean number of pellets hoarded per rat *per minute* in ten tests was 4.1. That is an average of 123 per half-hour. Taking only the four males in order to eliminate the possibility of having the result influenced by deficits due to pregnancy, we still have 2.4 pellets per minute, or 71 per half-hour.

It is not clear to us why Wolfe's demonstration of vigorous hoarding by non-deprived rats has not had more influence upon the development of hoarding theory. On the basis of subsequent observations, for example, it was concluded that hoarding is "primarily the result of food deprivation" (11, p. 292), that "the only condition which seems to be a necessary one for hoarding is that the animals undergo some food deprivation a short time before the hoarding tests are made" (13, p. 21). The crux of the matter, perhaps, was the shift from Wolfe's (15) open alleys to the closed ones less conducive to hoarding, that were used in Hunt's (4) and in most of the subsequent experiments. If our evaluation is correct, Wolfe's paper was of more than exploratory significance; it took Bindra's rediscovery of open alleys to show again that deprivation is a facilitating but not a necessary condition for hoarding.

It is relevant, however, to inquire why, after seeing so much hoarding by satiated and nondeprived rats, Wolfe did not himself stress the implications of his observations, instead of saying merely that they "showed that food-storing by rats was capable of quantitative investigation" (15, p. 108). The reason, it appears, is to be found in the results of two subsequent experiments reported in the same paper. In the first of these, Wolfe found that previous experience with pellets favored hoarding. Rats fed powdered food from age 20 days to age 40 days (and tested immediately thereafter) carried, on the average, only 1.2 pellets per 20-min. period, whereas rats brought up on pellets carried 3.4. In the other experiment, dietary deficiency proved to be an important factor in hoarding. Rats provided with an abundance of Chow plus supplementary foods from age 20 days to age 40 days carried an average of only 0.3 pellets, whereas other rats given inadequate food during the same period carried 16. Wolfe concluded that

The fact that rats raised on a diet sufficient in quality to enable them to reach maturity, reproduce, and appear normal in every way will readily store food even when non-hungry while other rats given a more complete diet will not indicates that the absence of certain food elements provides distinct motivation for specific behavior (15, p. 107).

Now it is possible that Wolfe's interpretation is correct, and that rats would never hoard pellets if they were always fed all they needed of every usable food element. If so, our conclusions about hoarding without deprivation are incorrect, but deprivation takes on a meaning very different from the one it has acquired in connection with the deficit theory of hoarding. In view of what the manufacturer says about the adequacy of Laboratory Chow as a diet for rats,² however, it appears at least equally possible that even the most carefully

TABLE 2
MEANS AND STANDARD DEVIATIONS, IN DECILOG UNITS, ESTIMATED FROM CUMULATIVE
DISTRIBUTIONS OF THE TOTALS FOR EACH RAT

GROUP	BEFORE DEPRIVATION				AFTER DEPRIVATION			
	Mean	S.D.	N	S.E.	Mean	S.D.	N	S.E.
I	—	—	10	—	15.3	3.4	8	1.2
II	8.2	4.3	9	1.4	15.0	2.8	4	1.4
III	13.2	4.7	9	1.6	18.9	4.2	9	1.4
IV	14.2	4.6	10	1.5	20.0	5.2	10	1.6
V	15.4	4.7	10	1.5	18.8	8.3	10	2.6
VI	20.1	5.6	10	1.8	23.6	2.4	10	0.8
VII	19.7	3.8	9	1.3	23.7	3.6	8	1.3

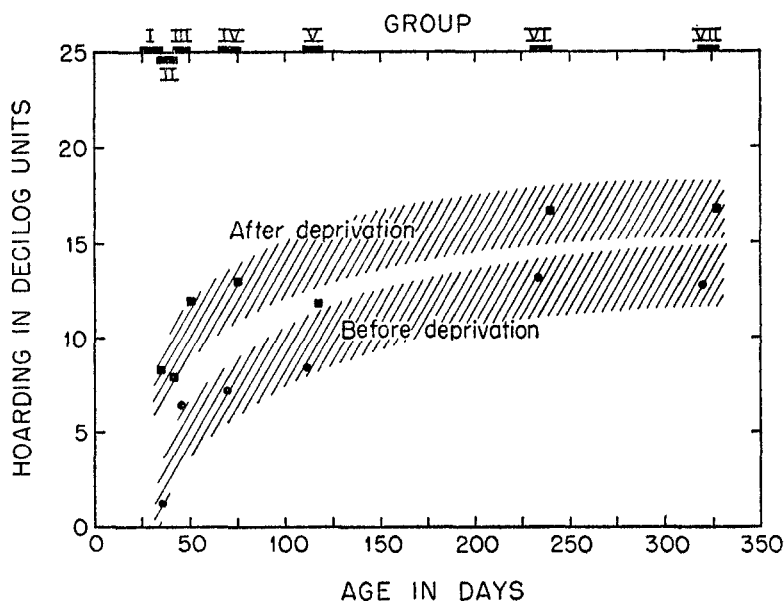


FIG. 2. TENDENCY-TO-HOARD AS A FUNCTION OF AGE

The ordinates are means for the various age-groups, estimated from cumulative distributions of the log-transformed totals for individual rats. Since the logarithmic transformation of the totals makes variability approximately constant from group to group, the shaded areas, which are 2 standard-error units in width, provide an indication of the uncertainty in the determination of the functions relating hoarding to age.

supplemented diet would not keep adult rats from hoarding under otherwise favorable conditions. The difference between the scores of Wolfe's 40-day-old rats and the scores of his 120-day-old rats may have been due mainly to the difference in age.

STATISTICAL ANALYSIS

In order to obtain an estimate of the reliability of the functions relating hoarding to age, we have employed a modification (5) of the procedure suggested

by Morgan (9). The procedure involves a logarithmic transformation of the hoarding scores. After the transformation, the variance of the scores is essentially homogeneous throughout the experiment, as shown in Table 2. This makes it possible to summarize the analysis in the way shown in Figure 2, in which the crosshatched areas are 2 standard-error units wide.

Two technical points about the statistical analysis and one incidental statistical result will be mentioned briefly:

Morgan's equations (9, p. 250) suggest that he used, as a regression line from which to read off the standard deviation of the transformed hoarding scores,

TABLE 3
AVERAGE RANK CORRELATIONS SHOWING RATS' TENDENCY TO MAINTAIN RANK THROUGH SERIES OF FIVE TESTS

GROUP	BEFORE DEPRIVATION		AFTER DEPRIVATION	
	ρ_{av}^* (1)	P (2)	ρ_{av}^* (3)	P (4)
I	—	—	.03	—
II	.06	—	.38	—
III	.22	.05	.42	.01
IV	.12	—	.57	.01
V	.34	.01	.67	.01
VI	.66	.01	.38	.01
VII	.14	—	.37	.01

* Determined from coefficient of concordance, W , which is discussed in reference 6, pp. 410-415. For five tests of the same rats, $\rho_{av} = (5W - 1)/4$.

TABLE 4
THE CONCORDANCE OF THE HOARDING SCORES OF RATS FROM THE SAME LITTER

	BEFORE DEPRIVATION	AFTER DEPRIVATION	OVER-ALL
Coefficient of concordance, W	.52	.28	.33
Average rank correlation, ρ_{av}	.40	.10	.26
Level of significance, P	.01	—	.01

the line that minimized the squares of the deviations in the horizontal direction, i.e., deviations in number of pellets hoarded. Not following the rationale of that procedure, we used the line of regression of cumulative frequency on number of pellets hoarded.

We investigated the assumption, implicit in Morgan's procedure, that two tests of the same rat provide the same information as one test each of two rats. One would not assume, on a priori grounds, that such would be the case, and, indeed, it appears not to be for our data. Table 3 shows that the rats tend to maintain their ranks through the series of five tests, especially after deprivation. The 50 scores on which one mean in Figure 2 is based are therefore not mutually independent; there are not 50 (and not 49) degrees of freedom. The modified procedure used by Hunt *et al.* (5) avoids this difficulty.

The data of the experiment are relevant to the question: Are the rats of the same litter more nearly alike than rats of different litters, insofar as the tendency to hoard is concerned? Restricting our attention to seven of the ten litters and to age-groups III through VII (in order to obtain complete matrices), we have (a) ranked the rats of each age group on each test, (b) computed coefficients of concordance for the tests before deprivation, for the tests after deprivation, and for the over-all experiment. The coefficients, together with the corresponding average rank correlations, are shown in Table 4. The rank correlation between the pre-deprivation rank totals and the post-deprivation rank totals (not shown in the table) is $\rho = 0.61$. From these results, it would appear that in our experiment, especially in the pre-deprivation tests, there is a significant correlation within litters. It must be attributed either to constitutional factors or to experience prior to weaning. After they were weaned, the rats were not caged in litter groups.

SUMMARY

In an attempt to determine the relation between hoarding and age, we tested seven groups of rats, the youngest shortly after weaning, the oldest at 318 to 328 days of age. The central tendency of the relation increases with age in a negatively accelerated manner, the number of pellets increasing more or less linearly with the logarithm of age. This is the case whether or not the rats have been deprived of food before the hoarding tests. Although the general level of hoarding activity is higher after deprivation than before, the results confirm the observation that deprivation is not a necessary condition for hoarding.

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